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POPULATIONS OF BAY-BREASTED AND CAPE MAY WARBLERS DURING AN OUTBREAK OF THE SPRUCE BUDWORM

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Densities of both the Bay-breasted Warbler (*Dendroica castanea*) and the Cape May Warbler (*D. tigrina*) are generally believed to undergo striking local increases during outbreaks of the spruce budworm (*Choristoneura fumerifana* Clem.), an important defoliator of northern coniferous forests (e.g., Kendeigh 1947, Hensley and Cope 1951, Stewart and Aldrich 1951, 1952, MacArthur 1958, Morris et al. 1958). However, none of the studies have combined censuses of the birds, measurements of the birds' food supply (budworms), and descriptions of the detailed foraging patterns of the birds. I made observations on Bay-breasted and Cape May warblers during June 1976 in the Aroostook Valley, Aroostook and Penobscot counties, Maine, an area experiencing heavy defoliation by budworms during 1976 and the 2 preceding seasons. In particular I sought to document these birds' foraging patterns, their population densities, and the densities of other *Dendroica* species during a period when it could be easily demonstrated that a superabundant source of food was available.

STUDY AREA AND METHODS

The study area was in northern Maine and centered about 46°23′N, 68°44′W; where Township 8, Range 8; Township 8, Range 7; (Penobscot Co.) and Township 9, Range 7; (Aroostook Co.) adjoin. This site is on the south bank of the Aroostook River where it is joined by Lapomkeag Stream. I conducted most of the study within an area of 15 km^2, but carried out additional observations elsewhere within these 3 townships.

The study area consisted mostly of second-growth balsam firs (*Abies balsamea*) and red spruces (*Picea rubens*), with smaller numbers of quaking aspens (*Populus tremuloides*). These trees generally reached a maximum height of 18–24 m and for the most part had a rather open understory (Fig. 1a). This vegetation predominated in the lower, well-drained parts of the area, but on higher ground considerable numbers of deciduous trees (primarily red maple [*Acer rubrum*], sugar maple [*A. saccharum*], yellow birch [*Betula lutea*], and beech [*Fagus grandifolia*]) occurred as well as the firs and spruces (Fig. 1b). On low, poorly drained soil northern white cedars (*Thuja occidentalis*) occurred frequently among the other conifers. No pesticides had been applied to the areas where the study was carried out (D. A. Stark in litt.).

Methods used generally followed those of earlier studies (Morse 1968, 1976). Briefly, I measured the amount of time that given individuals spent foraging at different heights and parts of the trees (tip of foliage, inner part of the limbs, etc.). A maximum of 5 min of foraging was taken per individual (usually it was not possible to obtain this much information before a bird was lost). Since these data were seldom gathered in the

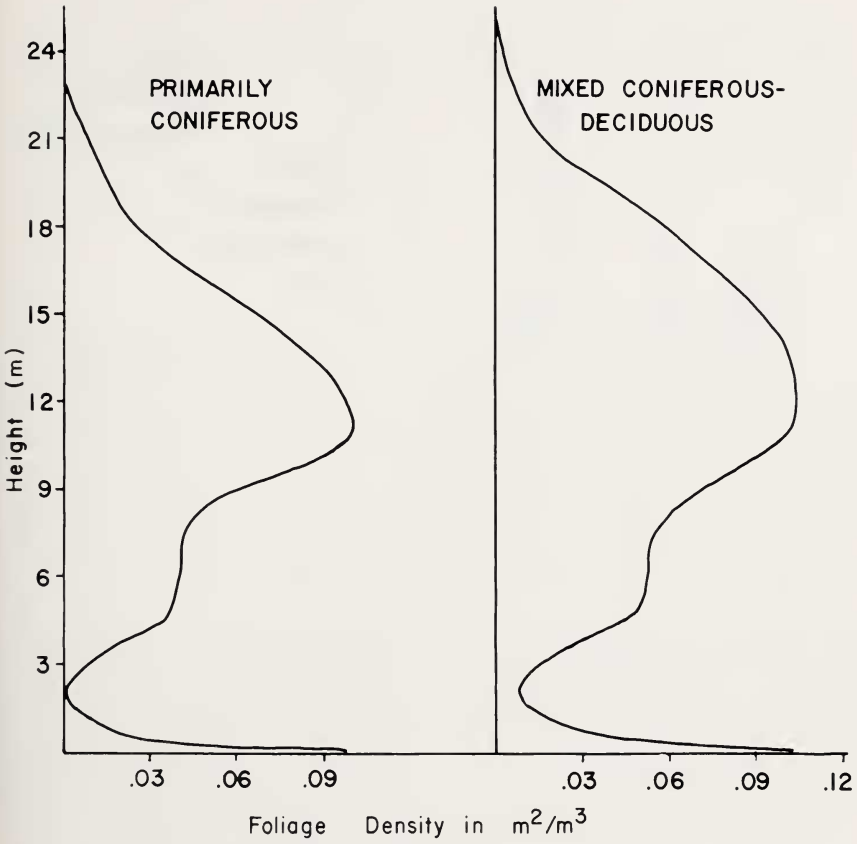

FIG. 1. Profile of foliage in the 2 census areas.

same area more than once, little if any duplication of individuals occurred. These observations were made upon males for the most part. Since many individuals were first located by their songs, it is possible that their foraging patterns at this time differed from the ones they usually used. However, when the data from the first minute of foraging were compared with those gathered subsequently, no significant difference appeared ($p > 0.05$ in a χ^2 test), so all data were combined.

Densities of breeding birds were established in 2 study plots, both 3.3 ha in size. One area was primarily coniferous (88%), while the other contained a considerably higher proportion of deciduous growth (only 60% coniferous). Eight censuses were made in each area, each lasting for nearly an hour. Where individuals held territories at the edge of the plots, I counted the number of observations made inside and outside the study area and assigned the bird in question a fraction of total occupancy.

Earlier studies on *Dendroica* warblers (Morse 1976) showed no simple relationship between total insect biomass and population sizes of insectivorous birds, but did establish

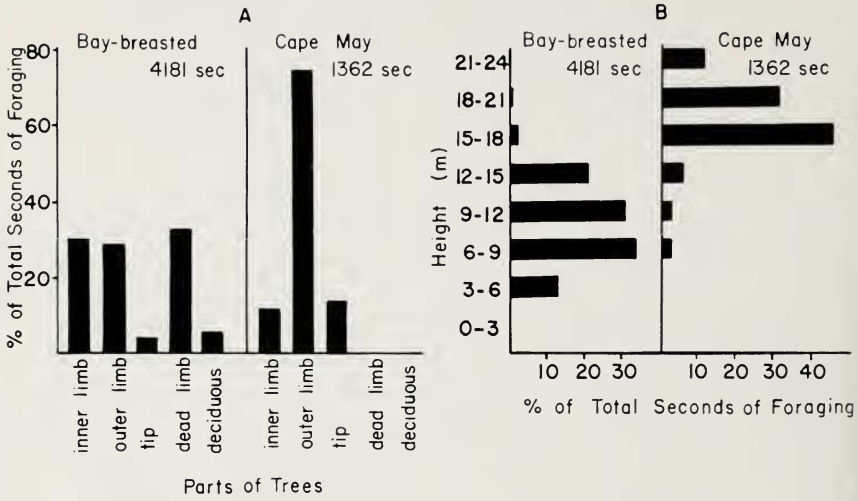

FIG. 2. Percentages of time spent foraging in different parts of tree; heights at which foraging took place.

that these birds took lepidopteran larvae at a rate far in excess of these insects' abundance. Mitchell (1952) and Dowden et al. (1953) have demonstrated a heavy intake of budworms by Bay-breasted and Cape May warblers when those prey were abundant. For these reasons and because of the extremely high densities of budworms in the present study, I confined measurements of food to the numbers of budworms present. These included counts of larvae and pupae in the canopy. I could also locate a high percentage of the budworms in their webs on exposed branches by viewing from the ground with binoculars. These censuses provided a second measure of abundance.

RESULTS

Foraging observations.—Bay-breasted Warblers concentrated their activities at medium to medium-low heights upon dead limbs and the inner parts of live limbs with little if any foliage, though they also foraged regularly upon the peripheral parts of live limbs in the midst of the foliage (Fig. 2). However, they spent little time exploring the distal tips of the vegetation (Fig. 2). They foraged upon red spruces more frequently (52.0% of observations) than would be predicted judging from the composition of the forests (Table 1) ($p < 0.01$ in a χ^2 test on the original observations). Cape May Warblers, on the other hand, concentrated their activities on the peripheral parts of the vegetation near the tops of the trees, though relatively little of their foraging time was spent upon the distal tips of the foliage (Fig. 2). They foraged even more heavily upon red spruces (71.2% of observations)

TABLE 1

COMPOSITION OF CANOPY TREES ON STUDY SITES (RANDOM SAMPLE OF 100 TREES)

Habitat	% fir	% spruce	% other conifers[1]	% deciduous
Primarily coniferous	54	34	0	7
Coniferous-deciduous	41	14	7	38

[1] Cedar, hemlock.

than did Bay-breasted Warblers ($p < 0.001$). Thus, based upon foraging locations alone, the 2 species segregated their activities almost completely, even though they both favored red spruces.

Relatively few foraging maneuvers other than gleaning were noted. Bay-breasted Warblers were observed to hawk for insects twice and to hover at the tips of vegetation twice. Cape May Warblers were observed to hawk twice.

Only a modest percentage of time was spent actively foraging. During

TABLE 2

DENSITY OF SMALL PASSERINE BIRDS ON STUDY SITE IN PAIRS/40 HA (100 ACRES)

Species	Site 1—primarily coniferous	Site 2—coniferous-deciduous
Wood Thrush (*Hylocichla mustelina*)	8	–
Hermit Thrush (*Catharus guttatus*)	11	–
Swainson's Thrush (*C. ustulatus*)	29	28
Golden-crowned Kinglet (*Regulus satrapa*)	48	–
Ruby-crowned Kinglet (*R. calendula*)	12	–
Solitary Vireo (*Vireo solitarius*)	–	2
Red-eyed Vireo (*V. olivaceus*)	9	4
Northern Parula (*Parula americana*)	–	12
Magnolia Warbler (*Dendroica magnolia*)	3	8
Cape May Warbler (*D. tigrina*)	12	1
Black-throated Blue Warbler (*D. caerulescens*)	–	41
Yellow-rumped Warbler (*D. coronata*)	12	–
Blackburnian Warbler (*D. fusca*)	12	35
Bay-breasted Warbler (*D. castanea*)	72	83
Ovenbird (*Seiurus aurocapillus*)	47	41
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	–	1
Purple Finch (*Carpodacus purpureus*)	–	7
Dark-eyed Junco (*Junco hyemalis*)	48	–
TOTAL	323	262

the process of gathering the foraging observations upon Bay-breasted Warblers (4181 sec), individuals showed no sign of foraging activity during an additional 6702 sec, either perching motionless or preening alternately between songs. Foraging thus constituted only 38.4% of the time during which males were observed. The ratio was even more extreme for Cape May Warblers. While 1362 sec of active foraging observations were made, 4139 sec of non-foraging activity were noted, with foraging in this case taking up but 24.8% of the time during which males were observed. Probably these figures are conservative in both cases, particularly for Cape May Warblers, since I frequently searched for considerable periods of time before locating singing birds. Most likely I did not sight them sooner because they were inactive.

Censuses.—Bay-breasted Warblers were common on both coniferous and mixed coniferous-deciduous census plots (Table 2). Contrary to expectation, however, concentrations were slightly higher on the mixed plot than on the coniferous plot. Cape May Warblers were much less common than Bay-breasted Warblers (Table 2). Furthermore, based upon these censuses and other observations, they were confined to low-lying areas composed primarily of tall red spruces and balsam firs. Only in one area visited did Cape May Warblers' territories closely adjoin each other.

Several other species of insectivorous birds occupied the 2 plots (Table 2), including other *Dendroica* species, as well as members of additional warbler genera and other passerine families. Of the 18 species cumulatively nesting on the 2 areas, only 6 were found on both. In both places the Bay-breasted Warbler was the most abundant species present. Of tree-dwelling warblers (*Dendroica* and *Parula*), only 3 of 7 species nested on both study areas (Magnolia Warbler, *Dendroica magnolia*; Blackburnian Warbler, *D. fusca*; and Bay-breasted Warbler), and of these, only the Bay-breasted Warbler was common on both. Of the other 6 tree-dwelling species (kinglets, vireos, grosbeaks, finches), only the Red-eyed Vireo (*Vireo olivaceus*) occurred on both areas, and then only at low density. Two of the 5 primarily ground-dwelling species (thrushes, ovenbird, junco) occupied both areas, both in relatively similar high density (Swainson's Thrush, *Catharus ustulatus*; Ovenbird, *Seiurus aurocapillus*). Therefore, Bay-breasted Warblers were among the few species, and were the only primarily arboreal species, that regularly nested in high density in both habitats.

Food supply.—I calculated budworm numbers in terms of individuals/branch. Virtually all branches inspected contained at least one budworm, and most branches in the crowns of trees contained several (Table 3). Using the estimated food demands of these warblers in the literature (George and Mitchell 1948, Mitchell 1952), one can calculate the approximate impact of

Table 3

Number of Budworms per Branch[1] on Study Sites (±1 s.d.)

Study site	Fir		Spruce	
	Larvae	Pupae	Larvae	Pupae
MANUALLY INSPECTED				
Primarily coniferous	3.3 ± 0.7	5.3 ± 0.9	3.6 ± 0.8	2.0 ± 0.6
VISUALLY INSPECTED				
	larvae and pupae		larvae and pupae	
Primarily coniferous	4.0 ± 1.1		3.4 ± 1.0	
Coniferous-deciduous	5.6 ± 1.2		4.1 ± 1.1	

[1] Based upon a total of 10 branches from 5 different trees.

the birds upon the resource (Table 4) and whether this resource is likely to become limiting.

Even the maximum likely intake involves only a small part of the budworm population (Table 4). The actual intake probably falls nearer the minimum likely intake (Table 4). Thus, this single resource turns out to be sufficient to support the entire bird population several times over. These measurements thus suggest strongly that the birds have a superabundant food source, at least to the degree that they can survive solely upon this food source.

Table 4

Numbers and Exploitation of Spruce Budworms

	Site 1—primarily coniferous	Site 2—coniferous-deciduous
Spruce trees/ha	3722 ± 464.6	1260 ± 236.4
Fir trees/ha	2344 ± 292.4	430 ± 80.8
Branches/spruce tree	108 ± 10.4	–
Branches/fir tree	102 ± 10.1	–
Total budworms/ha	4,307,423	1,442,045[1]
Estimate number of budworms removed per ha by birds[2]	44,608–111,520	36,309–90,773
% of total budworms removed by birds	1.0–2.6	2.5–6.3

[1] Based upon the assumption that the visual scanning technique resulted in an underestimate, from comparison of these results with hand-sorting techniques from Site 1 (Table 3) used in the calculation of budworm numbers for that area, I have multiplied the spruce data by 1.2 and the fir data by 1.4.

[2] Maximum based upon estimate of 35,000 taken/acre/season by 2.5 pr./acre plus their young (George and Mitchell 1948). Minimum based upon 40% of the above, the volumetric proportion of budworms found in stomachs during a moderate infestation (Mitchell 1952).

DISCUSSION

Foraging.—The spatial placement of Bay-breasted and Cape May warblers relative to each other resembles that reported by MacArthur (1958). However, the foraging patterns of these Bay-breasted Warblers differed from those documented by MacArthur, in that individuals spent considerably more time on dead limbs, generally at a low height, than did MacArthur's birds. Initially, this type of behavior seems paradoxical for a bird that feeds heavily upon budworms, prey that, true to their name, concentrate primarily upon new growth. However, upon several occasions Bay-breasted Warblers were observed to capture budworms descending on their threads (probably locating new feeding sites, since this species typically pupates on the foliage; Morris and Miller 1954). Foraging upon dead limbs may thus be highly efficient for the bird; visibility is good because there is no foliage and the larvae are unable to retreat into their webs as they do when approached in the foliage. Put in this context, even remaining motionless in these locations may represent part of a highly effective feeding strategy on the part of Bay-breasted Warblers.

Since MacArthur (1958) did not report the density of lepidopteran larvae in his studies, it is impossible to account for the presently-noted discrepancy in foraging patterns of Bay-breasted Warblers in the 2 studies. However, the most likely explanation is that his birds were not experiencing high densities of budworms.

The foraging patterns of the Cape May Warblers, which concentrated on the distal (but not terminal) part of limbs high in the trees, would give them ready access to budworms. A considerable proportion of new growth on these coniferous limbs occurs on the tops of these branches.

Population density.—The densities of Bay-breasted and (particularly) Cape May warblers recorded in this study are lower than those reported in certain other studies in areas of budworm outbreaks (Kendeigh 1947, Hensley and Cope 1951, Stewart and Aldrich 1951, 1952), though higher than most (Erskine 1971, 1972, 1976). While numbers of Bay-breasted and Cape May warblers in this study exceeded those typical of non-outbreak situations (Sanders 1970, Erskine 1971, 1972, 1976), their density, plus that of the other *Dendroica* species in the 2 census plots, approximated those of the combined *Dendroica* species in coastal spruce forests not experiencing such an increase of insect numbers (Morse 1976). This evidence suggests that even at this high food density, part of the change in insectivorous bird populations results from a substitution of species. Such a shift is consistent with Morris et al.'s (1958) observations that densities of several other species of *Dendroica* warblers decreased when those of Bay-breasted Warblers

increased. On the other hand, Sanders (1970), censusing areas where Kendeigh (1947) had worked earlier, found that bird populations in the absence of a budworm outbreak were very similar to those found by Kendeigh, except for the nearly complete absence of the budworm specialists.

Food supply.—It seems highly unlikely that the numbers of budworms were limiting the size of the population of either the Bay-breasted or Cape May warblers; censuses of budworm densities indicated that they were present in large numbers (usually several per branch) in both study areas. At this density only a small percentage of these insects was eaten. Further, the warblers spent only a minority of their time actively foraging, which suggests that they could have gathered far more food items than they did, if demands had existed for them. Though most observations were made upon males, which in the case of several congeners typically forage more slowly than their females during this period (Morse 1968, Black 1975), the high abundance of food militates against time restrictions providing a severe problem even for the females.

Population limitation.—This study does not permit a definite answer to the question of what factors place a limit upon the density of these species when food becomes superabundant. Most likely, however, the answer will be one of the following, or a combination of them: (1) Numbers of birds are inadequate to populate the areas more densely. This possibility is consistent with reports by Kendeigh (1947), Hensley and Cope (1951), and Stewart and Aldrich (1951, 1952) of even higher densities of Bay-breasted warblers, Cape May Warblers, and overall bird populations in other budworm outbreaks.

(2) Budworms do not provide a complete diet for these birds. The data of Mitchell (1952), showing that in a somewhat lighter outbreak of budworms than the present one insectivorous birds (including the 2 species of warblers of particular concern here) consumed only about 40% budworms by weight, suggests that other foods may be important in the diets of these birds. On the other hand, since Mitchell's data were taken from denser bird populations than those studied here, nutrition seems unlikely to be of primary importance in regulating numbers at these lower densities.

(3) Territorial behavior may be limiting numbers. These birds were observed to chase and attack each other during this study, and references to similar behavior may also be found in other studies where superabundant food supplies existed (Kendeigh 1947, Morris et al. 1958). While such behavorial patterns may not seem adaptive under these conditions, they may be highly adaptive when resources are not abundant. Again, however, since other populations denser than the present ones have been reported, aggressive be-

havior cannot in its own right account completely for the population densities reported in this paper.

SUMMARY

The foraging patterns, food supply, and population density of Bay-breasted and Cape May warblers were studied during a budworm outbreak in the spruce-fir forests of northern Maine. Bay-breasted Warblers foraged more intensively on low dead limbs than previously reported, probably a result of searching for budworms descending on threads from higher in the canopy.

Cape May Warblers concentrated their activities in live vegetation near the tops of trees. Males spent no more than ¼ to ⅓ of their time foraging. Bay-breasted Warblers were the commonest species upon plots censused both in lowland spruce-fir forest and in upland forest containing up to 40% deciduous growth. Budworm numbers were far in excess of the food demands of these warblers or the insectivorous birds as a group.

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